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## HISTORY OF SCIENTIFIC STUDY ON A LARVAL COLOR POLYMORPHISM IN THE GENUS *CHLOSYNE* (NYMPHALIDAE)

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A STRIKING POLYMORPHISM involving larval color is manifested in two species of melitaeine butterflies, *Chlosyne lacinia* (Geyer) and *Chlosyne gorgone* (Hubner). Each species exhibits three morphs: 1) *rufa*, an orange form, 2) *nigra*, a black form and 3) *bicolor*, a black form with a row of orange spots along the mid-dorsal line giving the appearance of a broad stripe. The larval morphs of *C. lacinia* were illustrated in natural colors by Neck et al. (1971). The resemblance of the polymorphic larvae of these two species is remarkable. Genetic studies have revealed that the inheritance mechanisms are identical in both species (Neck et al., 1971; Neck, 1973b). The polymorphism is believed to be homologous in that it is probable that both species are derived from a common ancestor which was also polymorphic for larval color patterns (Neck, 1973b). Remarkably, there has been no scientific study of these polymorphisms until the past several years.

The difference between the comparable morphs of these two species are diagnostic but very minor. The *gorgone rufa* is a yellowish orange while the *lacinia rufa* is orange to orange-red. This is true as well for the stripe of the comparable bicolor morphs. The mid-dorsal spots of the *gorgone bicolor* are strictly square-like in configuration while the spots of the *lacinia bicolor* are more variable and less distinct in shape and tend toward ovoid in some individuals. The melanized portions of the bicolor morph and *nigra* morph of *gorgone* appear to be somewhat darker than the comparable portions of *lacinia* larvae. This results in a greater contrast between the dark background and the lighter stripe of the bicolor morph in *gorgone* than in *lacinia*.

## Larval Descriptions By W. H. Edwards

Edwards (1893) reported the initial description of *lacinia* larvae (as *Synchloe lacinia* Geyer) as quoted from a letter by T. D. A. Cockerell—"1. nigra, a black form. 2. bicolor, a black with broad dorsal stripe. 3. rufa, a red form." Edwards (1893) also described *lacinia* larvae in his own words as follows: "There are at least three distinct types of larva: 1st.—All red- or yellow-fulvous. 2nd.—The dorsum and lower part of side fulvous, the sub-dorsal areas dark brown. 3rd.—All black, or black with a greenish band on each side." Note the reversal of order of nigra and rufa.

The following year Edwards (1894) described samples of *gorgone* larvae (reported as *Phyciodes carlota* Reakirt) which he had reared simultaneously with the *lacinia* larvae. His description (from three larvae) fits the bicolor morph—"deep black . . .; a red-fulvous mid-dorsal band . . ." Although he received eggs from Colorado and larvae from Montana, most of his larvae entered diapause before maturing. His original samples may have contained individuals of one or both of the other morphs. The color polymorphism is quite muted in diapausing individuals.

It is surprising that Edwards did not refer to a resemblance of the bicolor larvae of these two species. Although he quoted from a letter by Cockerell in describing *lacinia* larvae, Edwards reared larvae of the two species concurrently. He further stated, "The eggs of the two are in no way distinguishable, nor are the larvae in the first two stages; as regards shape and armature they are alike in the succeeding stages, but differ in coloration." Edwards apparently did not consider the larvae to be similar due to the interspecific differences discussed above. Possibly, the larvae were affected by rearing conditions, long overland mail travel, or entered diapause, all of which are known to affect larval coloration.

Subsequent Descriptions of *lacinia* Larvae

Other less complete descriptions of the larvae of *lacinia* have appeared in the American scientific literature. Comstock (1927: 119) reported the larvae as being "so variable in color as to be described with difficulty. The range is from a solid black to a reddish-fulvous, with a variety of stripes and blotches." Later, Comstock (1946) reported the larvae of this species to be "extremely variable in pattern and color." Tinkham (1944)

merely referred to the "spiny caterpillars" of *lacinia*. Thorne (1962) mentioned that "the few orange caterpillars of *lacinia* were conspicuous among the dark *californica* larvae." It is quite likely that he overlooked the nigra *lacinia* larvae as they look much like the black larvae of *Chlosyne californica* (Wright) as described by Comstock (1929). Thorne makes no mention of bicolor-type larvae.

Descriptions of *lacinia* larvae originating from Latin American populations were also published. Koehler (1927) reported upon the biology of *lacinia* (as *Chlosyne saundersi* Dbl. & Hew.) from observations in northern Argentina at the southern edge of the geographical range of *lacinia*. He reported that the larvae vary from bright reddish brown to almost black. The dark form contained many spots, dorsal, lateral or both (an apparent reference to the bicolor morph). ("Su color varia de marron rojizo claro al casi negro. En la forma oscura observamos muchas veces manchas dorsales o laterales o ambas. . .") Dyar (1911) gives a perfect description of a rufa larva as follows: "Body red-brown, marked transversely with black lines, two on each segment behind the spines. . . ." This description was made from an inflated specimen originating from an undefined locality in Mexico. It is pertinent here to mention that *lacinia* is not listed in monographs on the nymphalid larvae of South America (Muller, 1886) or life histories of Mexican lepidoptera (Comstock and Vasquez, 1961).

#### Subsequent Descriptions of *gorgone* Larvae

Other larval descriptions of *gorgone* exist. Only shortly before the appearance of the paper by Edwards (1894), Dyar (1893) described what was apparently a rufa larva ("body brownish-red") although it might have been a variant bicolor as he further describes it "with a dorsal and subdorsal black shaded line." Handford (1933) described the diapausing behavior of *gorgone* larvae but he gave no phenotypic description. Leussler (1938-39) mentioned that the larvae of *gorgone* were easily reared but made no mention of larval phenotypes. Heitzman (1963) referred to the similarity of the "quite black" larvae of *Chlosyne nycteis* (Dbl.) to the larvae of *gorgone* without referring to the polymorphic nature of *gorgone* larvae.

One reference to the similarity of the larvae of *lacinia* and *gorgone* has been found. Cockerell (1914) described the bicolor and rufa of *gorgone* (as *Phyciodes ismeria* Bdv. & Lec.) from Boulder, Colorado. It is strange that the nigra morph was not also described as nigra is the most common morph in Kansas populations (Neck, 1974). Reference is made to the fact that the two morphs described for *gorgone* "nearly correspond to two varieties" of *lacinia*. The two morphs which Cockerell described are the same two which had been previously reported (bicolor by Edwards, 1894, rufa by Dyar, 1893). Apparently the trimorphic nature of the larvae of *gorgone* was not realized until the recent publication on the genetics of this polymorphism (Neck, 1973b).

Most general (Morris, 1862; Scudder, 1889:III, 1811; Holland, 1898, 1931; Klots, 1951) and regional (Macy and Shepard, 1941; Brown et al., 1957; Ebner, 1970; Harris, 1972) butterfly manuals repeated a description for *gorgone* which best fits a rufa larva but differs from the one above. This description originated from Boisduval and LeConte (1833:168) whose name *ismeria* is now relegated to a synonym of *gorgone* Hubner (see Dos Passos, 1969). The description refers to a larva which is "yellowish with three longitudinal black stripes." Edwards (1894) states that the description of *ismeria* larvae "has no application" to the *gorgone* larvae he reared.

This description, however, also closely fits the larva of *Chlosyne harrisii* (Scudder). The better fit of the larval description of *ismeria* may be significant in that the dispensation of this name has not been completely settled. Higgins (1960) felt that *ismeria* more closely resembles aberrant forms of *harrisii*. F. M. Brown (1974) felt that *ismeria* is a synthetic drawing, possibly a modification of *harrisii* or *gorgone*. The description of the larva gives some credence to the view that *ismeria* is some form of *harrisii* although a *harrisii-gorgone* hybrid is also a possibility. However, the supposed type locality of *ismeria*, Georgia, is more likely to be *gorgone* as *harrisii* is not presently known from localities that far south. A likely solution to this nomenclatural problem is that *ismeria* is an extreme form of *gorgone* as some contemporary *gorgone* are known from Georgia which closely resemble *ismeria* (Harris, 1972:264, color plate 7).



### Reasons for Lack of Study

It can thus be seen that of the three people who described the larvae of *lacinia* in detail, only one (Cockerell in Edwards, 1893) divided the larval forms into three distinct categories. Apparently only one person (again Cockerell) saw more than one morph of *gorgone*. Comstock apparently saw all three morphs of *lacinia*, but he did not separate them into three distinct categories. This may have been partially due to the effect of environmental factors and/or genetic modifiers which tend to produce a nearly continuous variation from a basically discontinuous genetic polymorphism (Neck, 1974). Koehler, like Comstock, did not take notice of the three morphs of *lacinia*, although it appears that this larval polymorphism of color patterns is also present in Argentine populations.

The phenomenon of polymorphism was not as widely discussed at the times of the above descriptions as it is now. This may partially explain the lack of distinction between larval morphs of *lacinia*. At the time of most early descriptions of larvae of these species there was little concept of polymorphism in the United States scientific community. Mendel's work had not yet or had just become known; forms other than the supposedly ubiquitous "wild-type" were considered sports. Later, the rise of the ecological genetics school in England saw work on *Panaxia*, *Biston* and *Cepaea*. From this beginning polymorphism has become one of the most discussed biological phenomena of today.

Interestingly, one publication (Edwards, 1893) includes the term polymorphism in the title. Here, however, the term is applied to variant forms of the adult phenotypes of *lacinia* (*adjutrix* Scudder and *crocale* Edwards and hybrids thereof), not to the larval stages. At that time attention for studies was focused (as it still is today, although to a lesser extent) upon imaginal forms. Larval descriptions were recorded for identification purposes, but these stages were often considered to be merely a stage required to produce the adult form and not a form with its own adaptive strategy. Cockerell (1914) referred to the larvae of *lacinia* as "polychroic."

The descriptions in Edwards (1893) were not picked up by most later workers. Higgins (1960) does not refer to this paper in his discussion of the larvae of *lacinia* although he does refer to the paper in other contexts. Holland (1898) in his first edition refers to the larvae as being "fully described by Edwards"

and follows with the correct reference (Edwards, 1893), but he does not repeat the larval descriptions. For some unknown reason he drops the mention of this description in his revised edition (Holland, 1931) and says nothing of the larvae of *lacinia*. As most subsequent national and regional butterfly treatments are based upon this work, subsequent guides say nothing of the larvae of *lacinia*. The reference was not completely lost, however, as Davenport and Dethier (1937) in their bibliography of rhopaloceran life histories listed this reference with respect to *lacinia*.

The long, unprecise description of *lacinia* larvae given by Comstock (1927) would not likely be republished by workers who would prefer a short, precise description for publication in a guide book. As this description was published in a regional butterfly book, it would not have received the wide distribution of a book of the scope of Holland (1898, 1931). In his book, Comstock (1927) does not refer to the Edwards (1893) reference, although he does make reference to it in a later paper (Comstock, 1946).

The lack of study of these larvae may also be related to the non-occurrence of *lacinia* and apparent uncommon occurrence of *gorgone* in those areas extensively studied by the early American lepidopterists, i.e. the northeastern states. *C. lacinia* occurs from Texas westward to southern California and southward to Argentina. *C. gorgone* ranges from Texas to Manitoba, occurring into the eastern Rockies particularly along water courses. It is also sporadically reported throughout the southern states to Florida and Georgia. An apparently isolated population of *gorgone* occurring in northern New York is the only known eastern record north of Georgia (Shapiro, 1974).

Both butterflies are opportunistic species of varying abundance whose larvae feed upon species of the family Compositae which are characteristic of highly disturbed habitats (Neck, 1973a and unpublished data). Much of the ranges of these species includes areas which are characterized by long periods of dry weather when butterflies are essentially non-existent. This is particularly true of the desert and semi-desert areas of southern California, Arizona, New Mexico and western Texas. This fluctuating pattern of population size may possibly have contributed to their being overlooked. Edwards (1894) remarks on the lack of study as follows: "Considering what a common

species *carlota* is over at least one-third of the territory of the United States, it is remarkable that so little has been published respecting it." He further notes that some of his correspondents found this species to be common, while others in the same region found it rare.

As neither of these species is an agricultural pest, there was no study by agricultural scientists. Although both feed on wild sunflowers, the commercial monocephalic sunflowers are not readily acceptable to *lacinia* (Neck, 1973a).

### SUMMARY

A striking polymorphism involving color polymorphism is exhibited by the larvae of *Chlosyne lacinia* and *Chlosyne gorgone*. These polymorphisms have remained unstudied until very recently because of a combination of factors. Their geographical ranges occur, for the most part, outside the areas most intensively studied by early American lepidopterists. A reference describing the polymorphic nature of one species was not utilized by later workers. Only recently was the complete polymorphic status of the other species described. Other descriptions referred to a single morph (in one case two morphs were described) or described a continuous variation of larval phenotypes. A problem of taxonomic nomenclature resulted in an erroneous description for *gorgone* in most butterfly texts. Characteristics of their population biology also tend to lessen the chances of study.

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